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MERISTIC HOMOLOGIES IN VERTEBRATES

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ONE of the most difficult problems in vertebrate morphology is to explain the serial homologies between the different groups. In the lower segmented animals these difficulties, although they exist, are far more simple and are far more easily explained. Thus no one has any doubt that the tenth or the fifteenth somite of *Homarus* is the exact equivalent of the serially homologous somite of *Cancer*. Between the larger Arthropodan divisions the task of comparisons of somites is possibly not so easy yet all attempts at drawing homologies between, say, a hexapod, an arachnid and a crustacean, are based upon the assumption of exact serial equivalency. It is true that one author or another has at times suggested the possibility of intercalation or elision of a somite, but these have been mere suggestions and have usually been discarded in the discussions.

In the vertebrates this comparison is more complicated. We are forced to assume that the shoulder girdle and fore limb of the frog are the homologues of those of man, although their connections are with entirely different somites when serial position is taken into account. In the case of the pelvic arch the numerical disparity of the corresponding somites is even greater, but in either case the identity of structure of arch and limb is so great that doubt of homology is practically impossible. How then has it come about that say the twelfth somite of the Amphibian is not homologue of the twelfth but of more nearly the twentieth of man?

In Gegenbaur's hypothesis that the girdles are derived from branchial arches and that these have migrated backwards over the post-cranial somites we have a possible explanation of these problems of the relations of girdles to body segments. The backward migration has been arrested at different points in the various

groups. But this explanation will not suffice for other cases, hence the probability that it is true for none.

In the frog as in all Ichthyopsida, there are but ten cranial nerves, while in the mammals there are twelve. There is no doubt that as far back as the tenth the nerves are exactly homologous in Amphibia and in the mammals. Relations to brain and to points of distribution place this beyond question, but what shall be said of the mammalian eleventh and twelfth? Are both of these nerves from the post-cranial region which have been transferred to the skull? If so, does it not follow that the cranium in the higher vertebrates is not the exact equivalent of that in the lower? and that the differences have been brought about by the transformation of cervical into occipital vertebræ. If this, in turn, be so, are the occipital bones of the frog homologous with those of the mammal? Or are the basi-, ex- and supra-occipitals of the one merely analogous of those of the other? Is Huxley's argument for the derivation of the mammals from the Amphibia because of the double occipital condyles in the two groups based upon analogies rather than on true homologies? Are the condyles in Amphibia and Mammals not homologous but rather homoplastic formations?

Carrying this matter further back in the body, how are we to explain that apparent shifting of the pelvis in such a form as *Necturus* as described by Bumpus, Parker and others? Are somites ten, twenty and the like exactly equivalent in the normal and aberrant forms? And has there been an actual shifting of the pelvic girdle from one somite to the next in some individual? Or has there been an actual intercalation of vertebræ, the one to which the ilium is attached being constantly the same morphologically if not serially? Or, lastly, have the limbs and their arches arisen from a continuous fin fold and has every somite which contributes to that fold the potentiality of limb formation with all that this implies?

To take another case. In *Amphioxus* there are a large number of gill slits, a number which is doubled during development by the formation of the 'tongue bar.' Right behind the last gill slit comes the entrance of the hepatic duct into the alimentary tract, there thus being no œsophagus nor stomach intervening between

the pharynx and the liver. Is this to be explained by saying that in the vertebrates the posterior gill clefts of *Amphioxus* have closed and that the space which they occupy has become converted into stomach and œsophagus? In other words are these formations of the vertebrate tube the homologues of a part of the gill region of the acraniate?

Then, too, what are to be done with cases of increased numbers of gill slits; the Notidanids with six or seven, the Californian *Bdellostoma* with its variable number, and *Amphioxus* itself? This question is wholly apart from that which discusses the relations between metamerism and branchiomerism.

Numerous other similar questions will readily suggest themselves to all. There is no reason for enumerating them here. The problem is, how are they to be explained. Must we find a separate explanation for each or can we find some one principle which will account for all?

This article is to be regarded in the light of a suggestion rather than a full reply with demonstrations of validity. I have no proof, other than analogies and the fact that the hypothesis here presented answers all the demands of the problem, that the explanation here advanced is the true one. It must be tested and the tests are not easily made.

In the invertebrate segmented animals there is, at the beginning, no metamerism. It appears later during growth, and in numbers of forms it is found that the segmenting tissues are produced by budding from groups of cells at the posterior end of the embryo. These are most familiar in the annelid teloblast and are scarcely less well known in the Insects and Crustacea. Their number varies between wide limits, but for the present purposes the most important points concerning them, aside from their budding capacities, are their position in a more or less plainly marked transverse band and their situation at the extreme posterior limit of the growing embryo. Extensive examination of the literature has not shown similar budding cells in the Cuvierian group of *Articulata* in other places than the tip of the growing embryo, with the exceptions noted below.

It follows then that in these teloblasts and their equivalents are the full potentialities of the future somites. From them arise

all the cells which are utilized in every structure which is metamorphically repeated, the material for the new somite not being budded from any pre-existing somite, but always just in front of the hinder end of the body.

This applies strictly to all cases which are known to me in the arthropods as well as to most of the annelids; but in a few of the latter group modifications occur in the process which have great interest for us. As is well known in a number of annelids asexual reproduction by transverse division occurs. At one or more points in the body a new head may develop with the eyes, appendages, etc., characteristic of the anterior end of the worm, these features arising from a somite which in its earlier stages is apparently normal and like its fellows on either side. Then, just in front of this new head the worm divides and two worms, each with fewer somites than the original one, are produced and from this time onward lead an independent existence.

Of these only the anterior worm need now be considered. After the separation the segment which was just in front of the new head of course becomes the terminal somite of the new worm. The worm now increases in length and the new somites are formed by material cut off from the terminal somite which thus must have within it the equivalent of the teloblasts of the embryo.

From these facts it seems logically to follow that at least certain somites in the body have the potentialities of forming material for additional somites and must contain within them the same physiological possibilities as the original teloblasts from which they arise. In other words, in the annelid before the beginning of the transverse division the capacity for producing new tissues was located at more than one point in the body, but it was not exercised until after the asexual reproduction was well advanced.

In the case of the *Naides* the somites thus produced are all similar in character but in such instances as *Protula*, where heteronomous somites occur, the division of the worm is accompanied by the formation of new somites which differ in kind.

The application of these facts to the various types of meristic variation which occur in annelids need not be discussed here, but I think it is apparent that they will in part explain some of them. I do not mean to say that they reveal first causes but they do point

out the mechanism involved and may be used to reduce all to a common rule.

In the same way the assumption that there are similar budding zones at various points in the vertebrate body will explain the various conditions outlined in the statement of the problem. In the vertebrates there is a continuous addition of new somites at the posterior end of the body as in the arthropods and annelids, implying the existence of the equivalents of teloblasts at the posterior end. The assumption of budding zones at other points will explain the other features noted. Such a zone in the occipital region will allow us to explain the difference in the number of cranial nerves in the mammals and in the Ichthyopsida and yet allow us to accept the homology of the occipital bones throughout the vertebrate series. The additional nerves are thus to be regarded not as transferred from the neck but as new or intercalated structures. In the same way we may explain the varying number of vertebræ in the different regions and allow at least one of the pelvic vertebræ to be regarded as a fixed point and may be relieved of any assumption of a shifting of the girdles. It will also explain many anomalies such as the attachment of the two halves of the pelvis to different vertebræ and the increased number of lumbar or thoracic vertebræ in man.

This is to be regarded solely as an hypothesis. So far as I am aware no one has seen such budding zones in any vertebrate. In fact it is extremely probable that there is no such well defined zone as is found in the band of teloblasts of the crustacean. It is to be regarded rather as a series of assumptions, based in part upon analogies, which, if true, would explain the questions with which the present note began. The hypothesis is presented as a suggestion to stimulate investigation and criticism upon an interesting and difficult subject.